NeuroReport 7,1909–1913 (1996)

Modulation of auditory and visual cortex by selective attention is modality-dependent

Peter W.R. Woodruff,[1,2,CA]
Randall R. Benson,[2]
Peter A. Bandettini,[2] Ken K.Kwong,[2]
Robert J. Howard,[1] Tom Talavage,[2]
Jack Belliveau[2] and Bruce R. Rosen[2]

[1]Institute of Psychiatry and King's College School of Medicine, Dept of Psychological Medicine, DeCrespigny Park, Denmark Hill, London, SE5 8AF, UK; [2]Massachusetts General Hospital, NMR Center, Dept. Radiology, Bldg. 149, 13th. Street, Charlestown, MA 02129, USA

[1,CA]Corresponding Author and Address

USING functional magnetic resonance imaging (fMRI), we investigated whether the response of auditory and visual cortex was modulated by attending selectively to either heard or seen numbers presented simultaneously. Alternating attention between modalities modulated fMRI signal within the corresponding sensory cortex. This study provides evidence that attention acts locally during early auditory cognitive sensory processing, and that modulation of auditory and visual sensory cortex by attention is modality-dependent.

Key Words: Auditory attention; Visual attention; Functional magnetic resonance imaging

Introduction

Selective attention to a stimulus is a prerequisite for conscious cognitive processing. Although it has long been recognized that attention modifies perceptual experience, debate about the interaction between consciousness and perceptual experience continues.[1,2] The site of brain activity responsible for conscious experience of sensory stimuli is largely unknown. However, there is evidence that activity in sensory cortex is influenced by cortical processes such as attention. Evidence from electrophysiology and neuroimaging in humans shows that attention to auditory or visual stimuli enhances neuronal activity and/or blood flow in primary and secondary sensory cortical regions that correspond to these modalities.[3,4] Attention to specific tones during dichotic listening tasks alters the electrophysiological response in auditory cortex.[5,6] Positron emission tomography (PET) and single photon emission tomography (SPET) neuroimaging during attention to phonetic quality *versus* pitch, and meaning versus emotional tone of words, has shown increases in left-sided temporal cortex blood flow.[7,8] Furthermore, the larger fMRI signal in auditory cortex following presentation of pseudowords *versus* words, and the dependence of signal on word presention rate, may be due to the greater attention required to process pseudowords and individual words presented quickly.[9] Similarly, studies of visual attention show that selectively attending to distinct attributes (shape, colour, velocity and position)[10,11] enhances blood flow in extrastriate cortex. Activity of sensory cortex by imagery in the absence of external stimuli provides further evidence for a causal link between conscious, attention- demanding cognitive processes and sensory brain regions.[12]

Is modulation of sensory cortex by attention specific to the modality of the stimulus? If so, which areas of the sensory system are sensitive to such modulation, and is this dependent on rate of stimulus presentation? We tested the hypotheses that, during simultaneous aural and visual presention of numbers, a) attention to those presented aurally would enhance auditory cortex activity, and b) that directing attention away from auditory towards visual stimuli would additionally modulate regions in occipital cortex.

Materials and Methods

Because attention effects may also be influenced by perceptual load,[13] we designed the experiment with seen and heard numbers 1–9 in both active conditions (Fig. 1). Each 6 minute experiment consisted of three separate epochs of 'attend auditory'

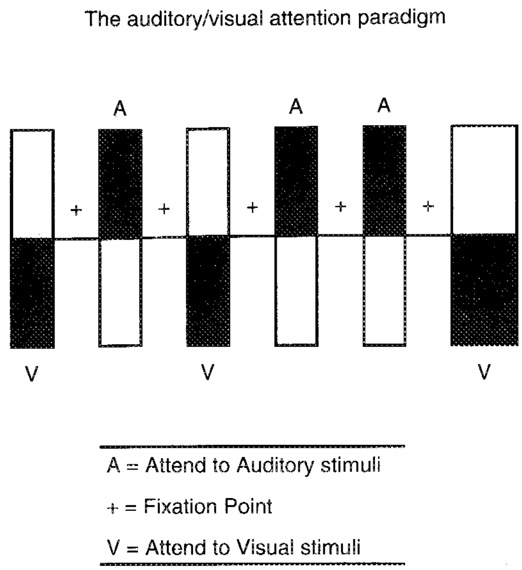

FIG. 1. The auditory/visual attention activation paradigm.

and 'attend visual' with baseline conditions of 'look at fixation point'. During 'attend' conditions subjects were presented with computer-generated pseudo-random numbers from 1–9, both visually and aurally at the same rate throughout (1.7 Hz), such that the number '8' would appear 20% of the time on average. No two simultaneously presented numbers were identical. Subjects were instructed to respond by pressing a keypress with their left index finger every time they heard (during 'attend auditory') or saw (during 'attend visual') the number 8. The keypress response of each subject to the target number was used to verify that tasks were performed correctly.

Alterations of eye position may influence activation of auditory and extrastriate visual cortex.[14] To minimize the potential for eye motion artefact, visually presented numbers and fixation point were centrally placed across all conditions. Scans were performed on right-handed subjects with no history of hearing difficulties. Four males (aged 29–38) and one female aged 34 were scanned using a surface coil (to maximize signal to noise) over the left temporal region (asymmetric spin-echo technique: TR = 1.2–1.75; 200 images per slice; 5 slices). Subjects were re-scanned so that nine studies in total were performed. In order to visualize both temporal and occipital brain regions simultaneously during the same session, head coil studies ($3 \times 3 \times 5$ mm, TR = 1.8–2.15, 170 images/slice, 8–12 slices) were performed on four males (aged 29–38). These subjects included two who had undergone the surface coil studies. All scanning was performed using a 1.5 Tesla GE Signa scanner retrofitted with ANMR instascan echo-planar imaging (EPI). Functional scans were aligned obliquely parallel with the Sylvian fissure through the brain. To assess motion, rectangular regions within the whole brain, left and right sides, were outlined on the third slice inferior to the Sylvian fissure. Percentage image intensity difference within these rectangles between the middle of the first and last baseline condition was used to determine movement drift during the course of the experiment. Experiments were excluded if drift exceeded 5% or the profile of movement included multiple peaks non-coincident with the paradigm. Anatomic regions were defined using a template for each slice on high resolution EPI images with the aid of a brain atlas.[15] Significant differences of intensity in brain regions between conditions were determined using the Kolmogorov–Smirnov statistic.[16] Coloured pixels exceeding a threshold ($p < 0.001$)[17] for the comparisons of 'attend auditory' and 'attend visual' conditions were superimposed on high resolution EPI images. Differences in mean image intensity level were taken from mid-points of conditions being compared at the beginning and end of the experiment. The mean of these two differences was used to calculate the % signal change within corresponding regions for a given slice. To verify the findings on individuals, an averaging procedure was performed separately on surface coil and head coil experiments from four subjects in each group. Statistical maps from the functional experiments were averaged, transformed into standardized Talairach space, and superimposed onto a similarly transformed re-sliced 3-dimensional spin-echo, T1-weighted, high resolution structural images (method adapted for MR from Fox *et al*[18,19]).

Results

Surface coil studies: One subject was excluded because of excessive intra-scan motion and this subject was not used for further surface or head coil experiments. Attention to the auditory versus visual component modulated primary/association auditory cortex activity in six of nine experiments (Brodmann's Areas [BA] 41/42), and auditory association areas (BA 21/22) in five of nine experiments. One of nine experiments showed no activity. Signal change within these regions ranged from 1.4 to 4.5%.

Head coil studies;
Results on scans on the same individuals during the same session indicated a shift in areas of activation from auditory to occipital cortex corresponding to the change from the 'attend auditory' to the 'attend visual' condition (Figs 2,3). When the images for the 'attend auditory' condition were compared with those of the 'attend visual' on invidual subjects, statis-

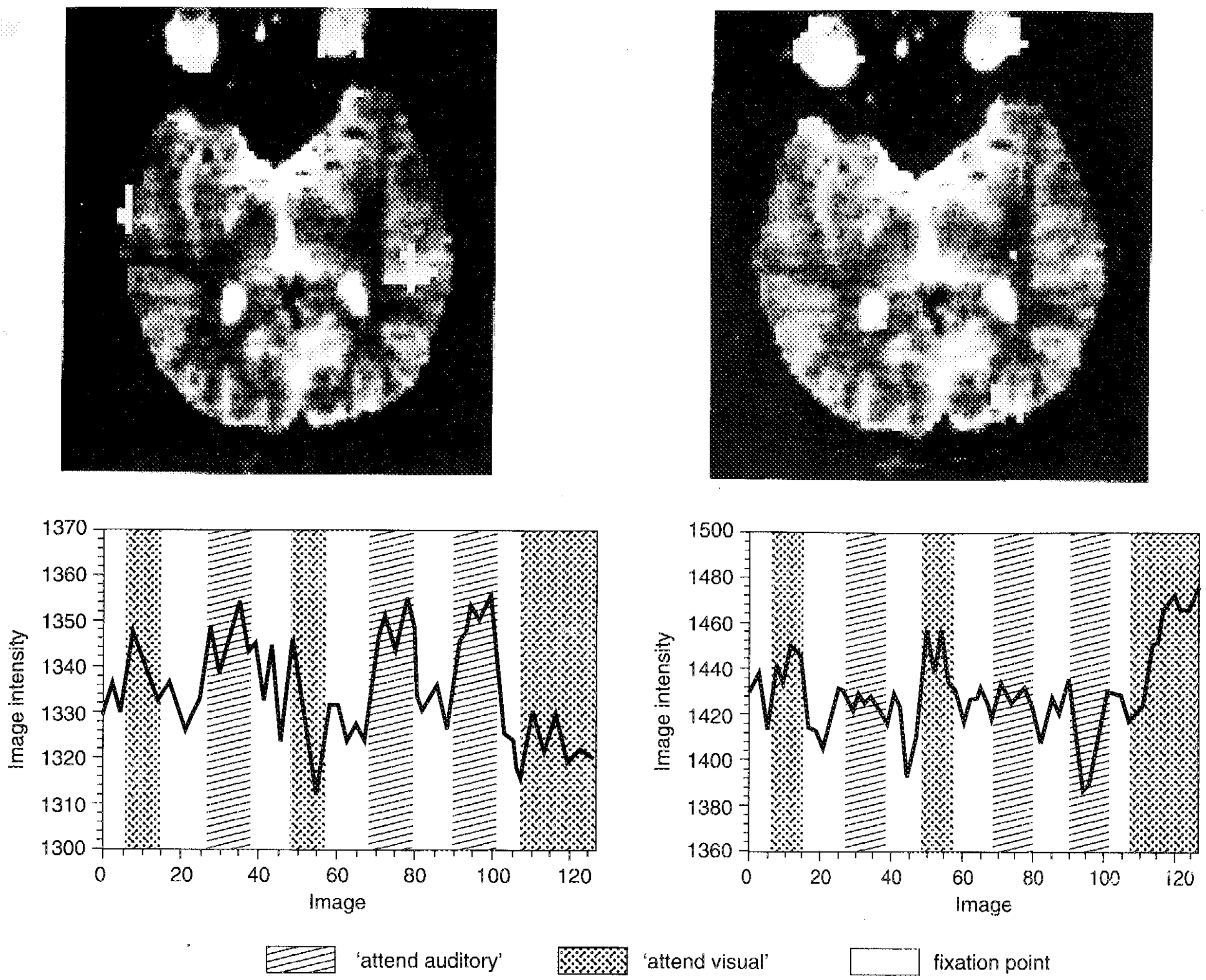

FIG. 2. Brain activation ($p < 0.001$) across identical slices through temporal and occipital lobes during the same session in one subject. Attention was directed to either: 1) auditory or 2) visual components of the simultaneously presented auditory and visual attention task. 1) Wernicke's area activated (right of image) and corresponding time course of image intensity. 2) Extrastriate visual cortex activation (posterior right) and corresponding time course.

tically significant differences were seen in the middle occipital and fusiform gyri.

The same comparisons as those made between 'attend auditory' and 'attend visual' applied to the averaged surface coil data revealed activations within BA 21 (x = −53, y = −44, z = 6; $p = 0.058$), BA 22 (x = −63, y = −2, z = 2; $p = 0.12$) and BA 42 (x = −63, y = −27, z = 10; $p = 0.013$; Fig. 4). The averaged head coil data showed a similar level of significance of activations in BA 21 (x = 57, y = −30, z = 0; $p = 0.058$) and BA 22 (x = 41, y = −50, z = 16; $p = 0.045$).

Examination of the averaged head coil studies revealed that modulation of visual cortex by visual attention of BA 18, BA 19, BA 37 and BA 39 just failed to reach statistical significance ($p < 0.15$). Posterior cingulate (p <t 0.05) (and cerebellar activation) was noted when activation during the attend auditory condition was "subtracted" from that of looking at the fixation point alone.

Discussion

Apparent activity around the eyes indicated probable eye movement synchronous with both 'attend' conditions (Fig. 2). Examination of the time course over eye regions, in contrast to those in the temporal and occipital lobes, revealed an artefactual pattern. We chose a high threshold level of significance for individual studies to reduce the possibility that these "activations" were due to type 1 error, but in so doing may have underestimated the attention modulating effect.

The modulatory effect noted may be due to enhanced activity in sensory cortex during corresponding attention conditions. Alternatively, selective attention to one sensory modality may be associated with decreased activity in cortical regions subserving the other modality.[20] In this case we may be observing a rebound hyperaemia in sensory cortex during selective attention to stimuli in the corre-

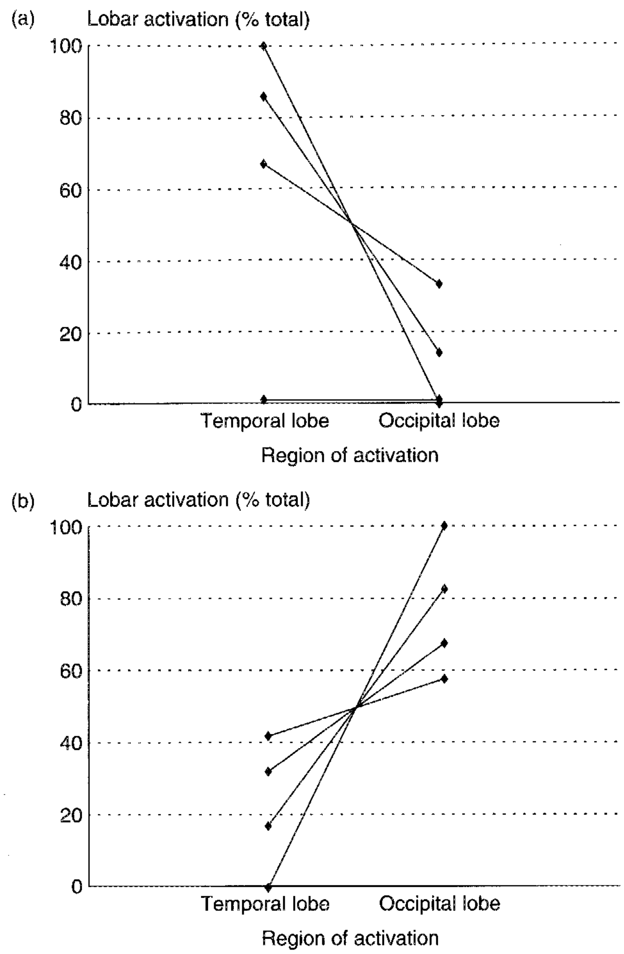

FIG. 3. The ratio of the extent of temporal to occipital lobe modulation by 'attend auditory' minus 'attend visual' as per figure (a) and 'attend visual' minus 'attend auditory' as per figure (b) for each subject whilst performing the task. The left ratio (as percent) = number of pixels ($p < 0.001$) in temporal lobe/(number pixels ($p < 0.001$) in temporal + occipital lobe). The right (ratio as percent) = number of pixels ($p < 0.001$) in occipital lobe/(number pixels ($p < 0.001$) in temporal + occipital lobe). Results from first experimental task of each subject shown.

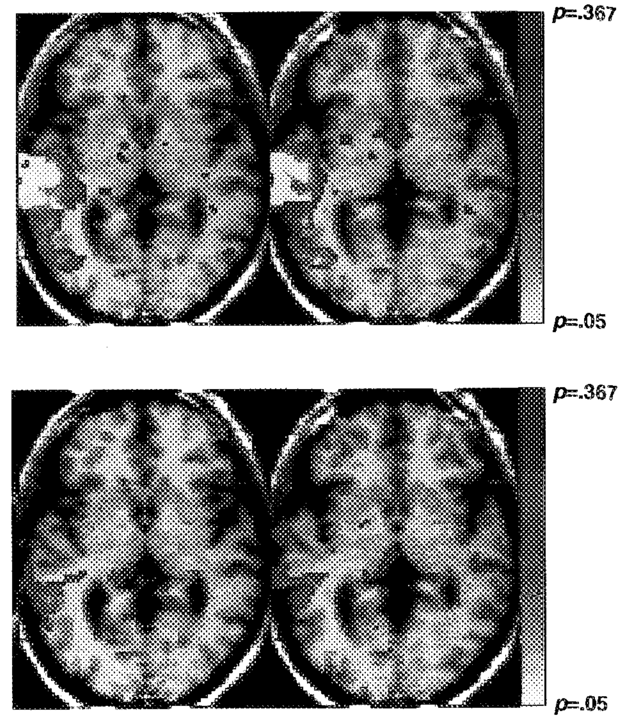

FIG. 4. Regions of activation in 'attend auditory' *vs* fixation point conditions (top row), and 'attend auditory' *vs* 'attend visual' conditions (bottom row) in two slices through the temporal lobe. Averaged left surface coil functional images from 4 subjects are superimposed on whole brain anatomic images.

sponding modality. Possible posterior cingulate 'activation' during fixation versus auditory attention could reflect such a rebound following key press response inhibition during the attention tasks.

Primary (BA 41) and nearby auditory association cortex (BA 42) is involved in early perceptual processing e.g. encoding and reconstruction of elementary features of stimuli.[9] Modulation by attention of these regions, where processing of auditory signal occurs, is consistent with physiological studies in monkeys[21] and those which have used event related potentials and magneto-encephalography in humans.[3,5,6] A mechanism akin to priming may underlie the blood flow changes we have described. Modulation of Wernicke's area by attention is similar to that observed when increased levels of semantic processing are required.[22] It is possible that attention enhances semantic processing required when presented with numbers.

Our results on individual subjects demonstrate that modulation of extrastriate visual cortex occurs in the presence of auditory distractors, and concur with those using positron emission tomography that multiple regions of extrastriate (but not primary) visual cortex are modulated by attention.[10,11] Modulation of fusiform gyrus by selective attention to a particular number is consistent with the observation that this brain region is concerned with perception of form.[11] The failure of the averaged data to show statistically significant modulation of regions in which modulation was demonsrated in individuals may reflect inter-subject variation in location of modulation within auditory and visual sensory cortex.

Conclusion

Our results support the theory that consciously driven attentional modulation operates at sensory cortical regions responsible for processing stimuli of the corresponding modality.

References

1. Block N. *Behav Brain Sci* **18**, 227–287 (1995).
2. Crick F and Koch C. *Nature* **375**, 121–123 (1995).
3. Hillyard A, Mangun GR, Woldorff MG *et al.* Neural systems mediating selective attention. In: Gazzaniga MS, Bizzi E, eds. *The Cognitive Neurosciences.* Cambridge, MA: MIT Press, 1995: 683–702.
4. Allport A. Visual attention. In: Posner MI, ed. *Foundations of Cognitive Science.* Cambridge, MA: MIT Press, 1993: 646–647.
5. Woldorff MG, Gallen CC, Hampson SA *et al. Proc Natl Acad Sci USA* **90**, 8722–8726 (1993).
6. Woldorff MG. Selective listening at fast rates: so much to hear, so little time. In: Karmos G, Molnar M, Csepe V *et al.*, eds. *Perspectives of Event-Realated Potentials Research (EEG Suppl. 44).* Amsterdam: Elsevier 1995: 32–51.
7. Kawashima R, Itoh M, Hatazawa J *et al. Neurosci Lett* **161**, 69–72 (1993).
8. Zatorre RJ, Evans AC, Meyer E *et al. Science* **256**, 846–849 (1992).
9. Binder JR, Rao SM, Hammeke TA *et al. Ann Neurol* **35**, 662–672 (1994).
10. Heinze HJ, Mangun GR, Burchert W *et al. Nature* **372**, 543–546 (1994).
11. Corbetta M, Miezen FM, Dobmeyer S *et al. Science* **248**, 1556–1559 (1990).
12. Le-Bihan D, Jezzard P, Haxby J *et al. Ann Intern Med* **122**, 296–303 (1995).
13. Lavie N and Tsal Y. *Percep Psychophys* **56**, 183–197 (1994).
14. Okita T and Wei J-H. *Psychophysiology* **30**, 359–365 (1993).
15. Talairach J and Tournoux P. *Co-planar Stereotaxic Atlas of the Human Brain.* Stuttgart: Thieme, 1988.
16. Tootell RB, Reppas JB, Dale AM *et al. Nature* **375**, 139[-[141 (1995).
17. Friston KJ, Jezzard P and Turner R. *Hum Brain Mapp* **1**, 153–171 (1994).
18. Fox PT, Perlmutter JS, Raichle ME *et al. J Comput Assist Tomogr* **9**, 141–153 (1985).
19. Breiter HC, Rauch SL, Kwong KK *et al. Arch Gen Psych (in press).*
20. Haxby JV, Horwitz B, Ungerleider LG *et al.* J Neurosci **14**, 6336–6353 (1994).
21. Goldstein MH, Benson DA and Hienz RD. In Woody CD, ed. *Conditioning: Representation of involved Neural Functions.* New York: Plenum, 1982: 307–317.
22. Price C, Wise R, Ramsay S *et al. Neurosci Lett* **146**, 179–182. (1993).

General Summary

It is generally thought that we need to selectively attend to stimuli in order to be consciously aware of them. We investigated whether selectively attending to the auditory or visual component of simultaneously presented auditory and visual numbers modulated blood flow in brain regions responsible for their perception. Attending to heard numbers modulated blood flow in brain regions subserving word perception. Attending to seen numbers modulated brain regions responsible for visual perception. The process of attending to stimuli in one modality rather than another appears to influence activity of brain regions concerned with perception within that modality.

ACKNOWLEDGEMENTS: We thank Prof. R. M Murray for his great support without which this study would not have been possible, we also thank Mr T. Campbell for technical assistance, Dr A.S. David for comments on the manuscript, and the Fullbright Commission and Mapother Award for financial support for PW. We acknowledge the support from the NIH (Grant number 5R01 MH 50054) and the Human Frontier Science Program.

Received 22 April 1996; accepted 23 May 1996